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## ORIGINAL PAPER

# Landscape heterogeneity and the confluence of regional faunas promote richness and structure community assemblage in a tropical biodiversity hotspot

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**Abstract** Crane flies (Limoniidae; Limoniinae) were sampled at national parks and protected areas across central to northern Thailand to observe patterns of species richness and faunal turnover in the Indo-Burma biodiversity hotspot. Prior to sampling, the crane fly fauna of this region was poorly known and no taxonomic keys existed for specimen identification. Utilizing a multi-access taxonomic key to the Limoniinae genera of the Oriental Region designed for this project, identification of collected specimens revealed a crane fly fauna displaying higher richness than inventories from temperate regions. Sixty-six morphospecies from 29 genera/subgenera were collected using a combination of light trapping and Malaise trapping. Richness estimators projected that a total of 70–81 species are to be collected with future sampling, with mountainous northern Thailand projected to have the highest richness. The faunas of Central and Northern Thailand were different, with the north generally composed of more temperate genera and the south composed of more tropical genera. The increased diversity in northern Thailand was significantly influenced by landscape topology. Sampling that spread across two mountain ranges displayed faunas that were divided into both high elevation (>1,000 m) and lower elevation (<1,000 m) faunas. This change in community assemblage across elevation illustrates faunas that

were more alike at similar elevations between mountain ranges than they were within national parks.

**Keywords** Biodiversity hotspot · Community assemblage · Limoniidae · Indo-Burma Hotspot · Tipuloidea

## Introduction

Estimating species diversity and understanding the impact of biotic and abiotic factors on richness and species' distributions are critical issues in conservation biology. These indices are especially important in biodiversity hotspots, where elevated richness is coupled with an increased rate of habitat destruction (Myers 1988; Myers et al. 2000). Within these areas, habitat loss due to deforestation or other anthropogenic effects serve as major threats to native biota (Laurance 1999; Sodhi et al. 2004). These threats are especially detrimental to Southeast Asian hotspots, which have some of the highest levels of species endemism with some of the highest rates of forest loss (Myers et al. 2000). For many faunal groups, especially extraordinarily diverse groups such as insects, the ability to measure diversity and determine species distributions within these areas may be limited due to a lack of taxonomic keys and trained experts.

A goal of tropical insect research, especially within biodiversity hotspots, should be to document patterns in diversity and community structure (Basset et al. 1998). Understanding the distribution patterns and ecology of hyperdiverse taxa will allow for monitoring of critical components of ecosystem functioning and may more efficiently detect environmental impact due to anthropogenic causes (Hilty and Merenlender 2000; Rohr et al. 2007). The ability to utilize insects for ecological monitoring and

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conservation planning relies on the existence of adequate taxonomic information and requires the capacity to distinguish and delineate taxa from one another (Hilty and Merenlender 2000; Issac et al. 2004; Mace 2004). Inventory of insect faunas across much of the tropics, however, is limited due to a lack of taxonomic keys, species descriptions, and a decrease in taxonomic expertise (Kitching 1993). These limitations are greatly accentuated due in part to the current taxonomic impediment (Taylor 1976). The taxonomic impediment describes the shortcomings in personnel and funding available for taxonomic study across much of the world, by which there exists a shortage of trained taxonomists and curators available to describe, organize, and conserve the world's organismal diversity. This greatly limits the ability to identify many insect groups to a meaningful level of resolution, resulting in incomplete food web reconstructions (Godfray et al. 1999) and the danger of species being lost before they have been documented (Lawton and May 1995). In order to document and monitor many taxonomic groups it will first be necessary to provide the basic tools for their identification (Evens and Winterton 2007).

Tropical insect faunas are known to be extraordinarily diverse, but remain largely under-sampled for many taxonomic groups (Godfray et al. 1999). Well-studied tropical insect faunas tend to possess clear ecological and economic importance (pollinators, agricultural pests), be taxa of medical or veterinary importance, or are considered 'charismatic entomofauna', that is insects that are typically large and ornate. Even for these well-studied groups there is a general lack of fundamental biological and ecological information pertaining to natural history, geographic distribution, and their role in ecosystem dynamics (Novotny et al. 2002; Lewis and Basset 2007). The species diversity of the remaining tropical entomofauna, however, has the potential to dwarf that of these better-studied groups, and will undoubtedly include many insects that play integral ecological roles (Kremen et al. 1993; Nee 2004; Rohr et al. 2007). Although difficult to study due in part to the taxonomic impediment, increased attention is being given to neglected tropical insect faunas because of their important roles in ecological processes and as indicators of ecological pattern and process (Pyle et al. 1981; Janzen 1987; Samways 1994, 2005).

This study examines the taxonomic richness and community assemblage of crane flies (Diptera; Tipuloidea) in the Indo-Burma biodiversity hotspot. With over 15,000 described species, crane flies represent one of the most species-rich groups of Diptera, itself being one of the four hyperdiverse insect orders (Lepidoptera, Hymenoptera, Diptera, Coleoptera) (Triplehorn and Johnson 2005). This globally distributed family occupies a diversity of habitats, both terrestrial and aquatic, that range from tundra to

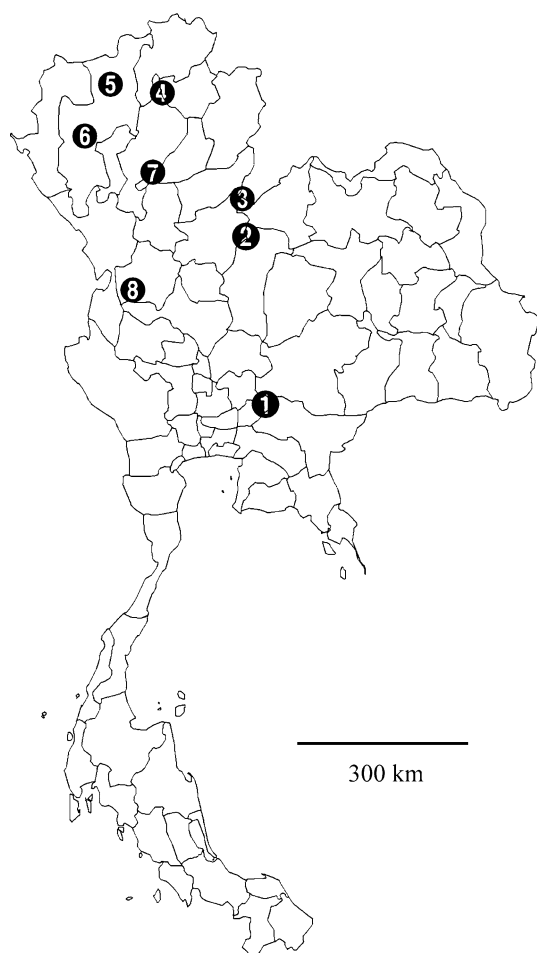
tropical forest, and often play an important role in ecosystem services and nutrient cycling (Pritchard 1983). Outside of well-studied areas (North America and Europe), the diversity of this group is largely contained as point locality data, with further distributional information absent due to a lack of basic taxonomic keys for specimen identification (see Papp et al. 2006). Although the biological affinities and geographic distributions remain poorly understood for most crane flies, species with restrictive biology (Godfrey 2000, 2001; Rotheray 2000) or strict association with unique habitats (Salmela and Ilmonen 2005) indicate that some species may represent important indicator taxa.

Here we examined the richness and community assemblage of Limoniinae crane flies (Diptera; Limoniidae) in Thailand while producing a taxonomic key for this and future specimen identifications. The subfamily Limoniinae represents one of the largest monophyletic crane fly clades (>5,000 spp.). The fauna of Thailand, like that of much of the Oriental Region, is poorly studied, being previously represented by only 18 species in 10 genera (Oosterbroek 2009). Other systematic crane fly inventories of equally sized or smaller temperate areas have shown much greater diversity [42 spp. Tennessee/North Carolina, USA (Petersen et al. 2005); 55 spp. Pennsylvania, USA (Young and Gelhaus 2000); 22 spp. Ohio, USA (Foote 1956)] and indicate that the crane fly diversity of Thailand is greatly underestimated. The goals of this project were to estimate the potential species richness for Thailand, examine the efficiency of different collection methodologies, and characterize the community assemblages and distributional patterns of crane flies across a network of protected forests in Thailand.

## Methods and materials

### Study area

Thailand represents an area of high faunal biodiversity and endemism that is coupled with high rates of habitat degradation and forest loss (Wilson 1988; Mittermeier et al. 1998; Myers et al. 2000). Located in the Indo-Burma Hotspot, which ranges from Nepal to Malaysia, Thailand's diverse geological and biogeographic history has resulted in a flora and fauna that represents a biotic interface between major biogeographic regions (Mittermeier et al. 1998). This project focused on collections made adjacent to lotic habitats in protected wildlife areas and national parks (NP) throughout central and northern Thailand (Fig. 1). These areas are situated around the central Chao Phraya River basin, along the Thanon Thongchai Range of northeastern Thailand (Doi Suthep, Khlong Lan, Doi Inthanon, Mae Ping NPs), the Phetchabun Range of north-central Thailand (Na Heaw and



**Fig. 1** Sample locations in Thailand. National parks (NP) and research centers where sampling was conducted included: Khao Yai NP (1), Phu Hin Rong Kla (2), Na Heaw NP (3), Doi Luang NP (4), Chiang Dao Research Center (5), Doi Inthanon (6), Wieng Ko Sai NP (7), Khlong Lan NP (8)

Phu Hin Rong Kla NPs), and Dongrak Range of the central Thailand (Khao Yai NP).

#### Sampling methods

The crane fly fauna of central and northern Thailand was sampled between 2000 and 2003 as part of a large-scale project to describe the aquatic fauna of this region. To this end, sampling was conducted at more than 100 stream, river, wetland, and waterfall locations. Collecting was conducted using a combination of hand collecting (netting, rock washing, detritus sampling) and structured sampling (Malaise trap, light trap). The sampling presented here represents a subset of these collections that were both (1) conducted at sites receiving multiple collection events over the course of the study and (2) used structured sampling techniques that were directed at the collection of adult insects. Therefore, single collection events or those

focusing on immature life stages were not included. These criteria resulted in the selection of 14 research locations (Table 1). Collections at these research sites were done using light trapping and Malaise flight intercept traps.

Malaise trap collections (MT) were made using 2-meter (long) by 2-meter (high) wet-head Townes style Malaise traps ([www.santetraps.com](http://www.santetraps.com)). Traps were placed in riparian areas alongside streams, with insects collected into jars of 70% ethanol. Malaise traps were run continuously for a period of approximately one year (Table 1) with collected samples emptied approximately every two to three weeks. Light trap sampling (LT) was conducted adjacent to streams using a combination of simultaneously run mercury vapor and black light methods. Generator powered mercury vapor lamps (160 W, 120 V) were placed over a suspended white sheet and illuminated after dusk and run for approximately 2 h, attracted flies were hand-collected off of the sheet and transferred into vials of 70% ethanol. Black light trapping was conducted using battery powered 15 W tube black light suspended over a pan of soapy water. The black light trap was allowed to operate overnight. The morning following black light collecting, collected contents were rinsed and transferred into 70% ethanol.

Sites were grouped into two different categories according to the type of sampling that was conducted at the location. Collection sites were divided between those that received only light trapping (LT) and those receiving only Malaise trapping (MT) (Table 1). The LT sites were used to characterize the community assemblage of the mountainous northern region of Thailand. The MT sites were used to categorize the community assemblage of a mountainous region of central Thailand (Khao Yai NP). One site at Phu Hin Rong Kla NP in north-central Thailand received both MT and LT sampling (2.1, 2.2) and allowed for a comparison of methods.

#### Sample processing

Collected specimens are housed at the Department of Entomology Insect Collection at Iowa State University. The subfamily Limoniinae used here is as defined by the Catalogue of Crane Flies of the World (Oosterbroek 2009) except for the inclusion of the genera *Atarba* (*Atarba*) Osten Sacken and *Atarba* (*Atarbodes*) Alexander. Specimens were identified to genus and subgenus using the *Key to the Adult Limoniinae Crane Flies of the Oriental Region, version 2.0* (Petersen 2007) constructed for this project. The key was constructed from a coded character matrix using Lucid© (CBIT; [lucidcentral.org](http://lucidcentral.org)) taxonomic key building software. Characters used for specimen identification were based primarily on wing venation and characteristics of the male hypopygium. Many taxonomic divisions are based on traits of the male and are not found

**Table 1** Collections from Thailand, 2000–2003

Site	Trap type	Collection details	Lat/long	Elevation (m)	Active dates
1.1	MT	Khao Yai National Park: Creek 2 km up Khao Khieo Road	14°22'N 101°24'E	950	vi.2000–x.2001
1.2	MT	Khao Yai National Park: Huai Patabak (km29)	14°19'N 101°21'E	505	vi.2000–x.2001
1.3	MT	Khao Yai National Park: Huai Tadapoo above Namtok	14°24'N 101°22'E	745	vi.2000–x.2001
2.1	MT	Phu Hin Rongkla National Park; Huai Man Daeng Noi at trail	16°57'N 101°03'E	1600	vi.2002–v.2003
2.2	LT	Phu Hin Rongkla National Park; Huai Man Daeng Noi at trail	16°57'N 101°03'E	1600	22–23.viii.2002; 27–28.ix.2002; 21–22.x.2002; 10–11.ii.2003; 20–21.vii.2002
2.3	LT	Phu Hin Rongkla National Park; Namtok Romglao	16°59'N 101°00'E	1190	20–21.vii.2002; 22–23.v.2002 10–11.iv.2003; 4–5.v.2003; 14–15.xi.2002; 17–18.i.2003
2.4	LT	Phu Hin Rongkla National Park; Waterwheel falls	16°59'N 101°00'E	1280	27–28.ix.2002; 22–23.vii.2002; 20–21.x.2002; 10–11.iv.2003; 20–21.vi.2002; 17–18.i.2003
3.1	LT	Na Heaw National Park; Namtok Tat Huang	17°33'N 100°59'E	500	9–10.iii.2002; 22–23.x.2002
4.1	LT	Doi Luang National Park; Namtok Pukaeng	19°26'N 99°41'E	540	26–27.ii.2003; 24–25.x.2002; 26–27.xii.2002
5.1	LT	Creek at Chiang Dao Wildlife Research Center	19°21'N 98°55'E	520	26–27.i.2003; 24–25.xii.2002; 27–28.ii.2003; 27–28.xii.2002; 13–14.x.2002
6.2	LT	Doi Inthanon National Park; Namtok Siripum (lower)	18°32'N 98°31'E	1380	2–3.iii.2002; 5–6.vii.2002; 15–16.x.2002; 16–17.x.2002
6.3	LT	Doi Inthanon National Park; Namtok Wachiratarn	18°32'N 98°35'E	650	16–17.x.2002; 3–4.iii.2002
7.1	LT	Wiang Ko Sai National Park; Lower Namtok Maekueng Luang	17°58'N 99°35'E	400	28–29.ix.2002; 22–23.vi.2003; 20–21.ii.2003; 25–26.x.2002
8.1	LT	Khlong Lan National Park; Namtok Khlong Lan	16°07'N 99°16'E	310	7–8.iii.2002; 19–20.x.2002; 24–25.ii.2003

Details for sites used as collection locations are given along with collection type (*MT* Malaise trap, *LT* Light trap) and dates (*MT* range between start and end of activity, *LT* dates of site visits, range of dates indicates overnight activity) of activity

in the corresponding female, resulting in a number of female specimens not being identified during this investigation. After being identified to genus/subgenus, specimens were then identified to morphospecies based on the recommendations of Krell (2004) by M.J. Petersen. Morphospecies are here described as separation of specimens into discrete recognizable groups based on morphological and/or coloration patterns.

#### Data analysis

It was not expected that all potentially available species would be collected during this work, because even with exhaustive sampling some species will avoid collection (Colwell and Coddington 1994). In order to estimate the potential number of species for the region, richness was estimated for LT, MT, and Thailand (ALL) using richness estimators (Incidence-Based Coverage, ICE; Chao 2; Michaelis–Menten Means, MMeans) that estimate total richness for a location based on the number of collected

species in relation to the number that were unique to that site (Colwell and Coddington 1994). Richness estimates were produced using EstimateS 8.0.0 (Colwell 2006). Different individual sampling events (LT, MT) do not produce equal sampling effort per collected sample and were not expected to accumulate specimens at an equal rate. Therefore, a measure of collected individuals was utilized as the index of accumulation. Sampling completeness was established by determining the percentage of species already collected in relation to the asymptote of the collection curve.

Individual LT sampling locations received different sampling intensities in the form of total sampling events per site (Table 1). All sites received at least two sampling events each occurring during the peak of adult fly emergence (February–June; September–December), but some sites received up to six total sampling events. Biased sampling could skew the observed community assemblage estimates by either artificially inflating or under-representing the morphospecies from a site; therefore, potential effects of number of samples taken per site on the number of

morphospecies collected were addressed using an ANOVA, implemented using JMP 7.0© (SAS Institute Inc.). Significance was assessed at the  $P < 0.05$  level.

Relationships among the community assemblages of northern Thailand (LT sites) and for all sites combined (ALL) at both the morphospecies and generic level were evaluated by non-metric multidimensional scaling (NMDS) in R-project (R Development Core Team 2004) with the *vegan* package. The similarity matrix used in NMDS was constructed using the Bray-Curtis index (Bray and Curtis 1957). Abiotic factors (latitude, longitude, elevation) and collection information (collection type) were fit to the constrained ordination using the *envfit* option and run with 9999 permutations.

## Results

### Observed diversity

Collections from all sampling techniques resulted in a total of 647 specimens representing 66 morphospecies from 29 genera/subgenera (Table 2). Twenty genera/subgenera were collected from Thailand for the first time and nine previously known genera from Thailand were recollected during this sampling. One genus of Limoniinae, *Limonia* Meigen, which was previously recorded from Thailand was not recollected. Details of morphospecies lists for individual sites are available from the corresponding author and are maintained with specimens housed at Iowa State University. Light trapping resulted in greater diversity than Malaise trapping and was responsible for 70% of all collected morphospecies. The number of morphospecies collected at each site during the LT sampling was not significantly influenced by number of sampling events per site ( $R^2 = 0.2554$ ;  $P = 0.1128$ ). The proportion of unique morphospecies at each site was positively correlated with elevation ( $R^2 = 0.6175$ ;  $P = 0.007$ ), with high elevation sites containing a greater proportion of total morphospecies as unique to that site (Table 3).

### Estimated diversity

Collection curves from individual sampling protocols (LT, MT) and ALL (Fig. 2) each failed to reach asymptotes. Asymptotic estimators indicate that ALL sampling was 94% complete with 66 observed morphospecies. MT sampling was 95% complete with 20 observed morphospecies, while LT light sampling was 88% complete with 46 observed morphospecies. Non-parametric estimators (CHAO2, ICE), which are partially influenced by the

**Table 2** Genera and subgenera found during sampling

Genera	Sites							
	KY	PHR	NH	DL	CDW	DI	WKS	KL
<i>Achyrolimonia</i> *	1	0	0	0	0	0	0	0
<i>Antocha</i> *	0	6	2	1	2	4	1	1
<i>Atarba</i> ( <i>Atarba</i> )*	0	1	0	0	0	0	0	0
<i>Atarba</i> ( <i>Atarbodes</i> )*	0	1	0	0	0	0	0	0
<i>Atypophthalmus</i> ( <i>Atypophthalmus</i> )	0	0	0	0	0	0	1	0
<i>Atypophthalmus</i> ( <i>Microlimonia</i> )*	1	1	0	0	0	0	0	0
<i>Dicranomyia</i> ( <i>Dicranomyia</i> )	2	2	0	0	0	0	0	0
<i>Dicranomyia</i> ( <i>Pseudoglochina</i> )*	1	1	0	0	0	0	0	0
<i>Dicranomyia</i> ( <i>Sivalimonia</i> )*	0	1	0	0	0	0	0	0
<i>Discobola</i>	0	1	0	0	0	0	0	0
<i>Elephantomyia</i>	3	1	0	0	0	0	0	0
<i>Geranomyia</i> *	2	6	1	0	1	3	1	3
<i>Helius</i> ( <i>Eurhamphidia</i> )*	0	1	0	0	0	0	0	0
<i>Helius</i> ( <i>Helius</i> )*	0	3	0	0	1	0	1	0
<i>Lechria</i>	1	0	0	0	0	0	0	0
<i>Libnotes</i> ( <i>Goniolineura</i> )*	0	2	1	0	0	0	1	1
<i>Libnotes</i> ( <i>Gressittomyia</i> )*	1	0	0	0	0	0	0	0
<i>Libnotes</i> ( <i>Laosa</i> )*	1	0	0	0	0	1	0	0
<i>Libnotes</i> ( <i>Libnotes</i> )	2	1	1	1	0	1	1	0
<i>Libnotes</i> ( <i>Neolibnotes</i> )*	1	1	0	0	1	1	0	0
<i>Orimarga</i> *	0	1	0	1	1	0	0	0
<i>Rhipidia</i> ( <i>Eurhipidia</i> )*	0	1	0	0	0	1	0	0
<i>Rhipidia</i> ( <i>Rhipidia</i> )	0	1	0	0	1	0	0	0
<i>Thaumastoptera</i> *	1	0	0	0	0	0	0	0
<i>Thryptomyia</i> *	1	1	0	1	0	0	0	0
<i>Toxorhina</i> ( <i>Ceratohelius</i> )	2	1	0	1	0	0	0	0
<i>Trentepohlia</i> ( <i>Mongoma</i> )*	2	1	0	0	0	1	1	0
<i>Trentepohlia</i> ( <i>Plesiomongoma</i> )*	1	0	0	0	0	0	0	0
<i>Trentepohlia</i> ( <i>Trentepohlia</i> )	0	0	0	0	2	2	1	0

Genera discovered during sampling of natural areas and national parks (NP) of northern and central Thailand are listed. Listed below each sampling location are the number of morphospecies of each genus found at that location (KY Khao Yai NP, PHR Phu Hin Rongkla NP, NH Na Heaw NP, DL Doi Luang NP, CDW Chaing Dao Research Center, DI Doi Inthanon NP, WKS Wieng Ko Sai NP, KL Khlong Lan NP)

\*Discovered for the first time in Thailand



**Table 3** Morphospecies collected at light trap locations

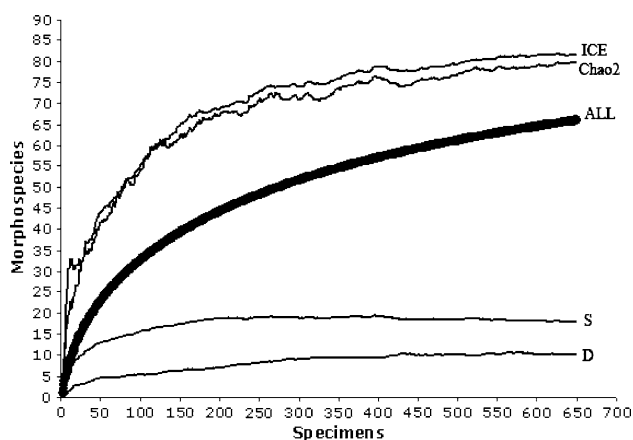
Site	Morphospecies	Uniques	Uniques (%)
2.2	17	8	47
2.3	6	2	33
2.4	12	3	25
3.1	5	1	20
4.1	5	1	20
5.1	9	1	11
6.2	11	7	63
6.3	3	0	0
7.1	8	2	25
8.1	5	0	0

The number and percentage of morphospecies collected by light trapping in northern Thailand as morphospecies unique to that location are given

presence of species represented by one or two specimens, provided higher estimates of potential richness for LT (CHAO2: 57 spp.; ICE: 57 spp.), MT (CHAO2: 21 spp.; ICE: 25 spp.) and ALL (CHAO2: 80 spp.; ICE: 81 spp.) sampling events than did MMMeans estimations (LT: 52 spp.; MT: 21 spp.; ALL: 70 spp.). All sampling events showed a reduction of singleton numbers with increased sampling, including a marked decrease by MT sampling. Singleton morphospecies represented 30% of total collected morphospecies in LT sampling and 25% of morphospecies for both MT and ALL samplings.

#### Regional faunas and biogeographic affinities

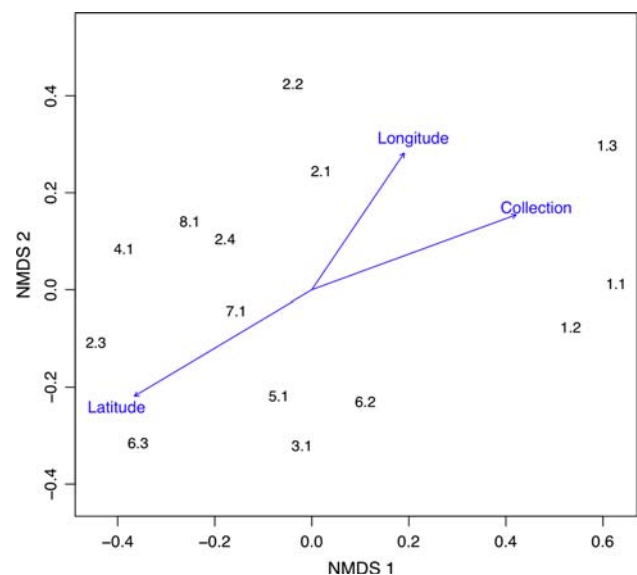
Most taxa collected from Thailand were from genera with widespread world distributions that are known from



**Fig. 2** Accumulation curve for crane fly sampling in Thailand. A species accumulation curve created using EstimateS is plotted showing accumulated morphospecies (ALL) plotted against accumulated specimens. Also plotted are curves for nonparametric estimators (ICE; Chao2) and morphospecies collected as singletons (S) and doubletons (D)

multiple biogeographic regions, but find their highest species richness in the lower latitudes (Oriental and Neotropical) (see Oosterbroek 2009). Observation of the Thailand (ALL) community assemblage showed a separation of Khao Yai NP MT collections from all other sites based on generic/subgeneric taxonomic resolutions (Fig. 3), but showed no separation based on morphospecies resolution. Across all sites, changes in morphospecies community assemblage were significantly correlated with elevation ( $P = 0.004$ ) and trap type ( $P = 0.030$ ) but not with longitude ( $P = 0.315$ ) or latitude ( $P = 0.127$ ). Changes in generic/subgeneric community assemblages were significantly correlated with latitude ( $P = 0.008$ ), longitude ( $P = 0.066$ ) and trap type ( $P = 0.003$ ) but was not correlated with elevation ( $P = 0.359$ ) (Table 4).

Light trap (LT) collections from northern sites were generally dissimilar in community assemblage caused by a large number of morphospecies unique to individual sites. Individual sites did not group strictly by geographic distance or national park, but instead responded to the landscape and altitudinal profiles of the region (Fig. 4) showing significant correlations with both elevation ( $P = 0.013$ ) and latitude ( $P = 0.049$ ) (Table 4). Locations were strongly divided between sites above 1,000 m and less than 1,000 m elevation. Generic community assemblage did not separate sites and no correlations were observed with abiotic variables.



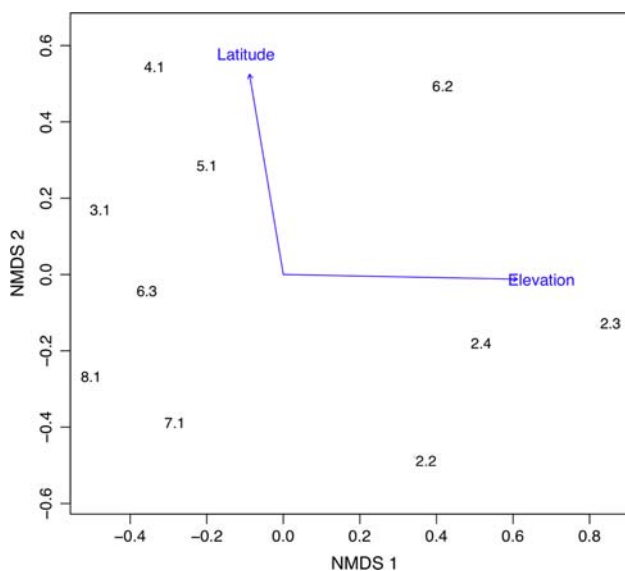
**Fig. 3** Non-Metric multidimensional scaling (NMDS) projection of sampling sites based on generic community composition. Collection codes refer to sites from: Khao Yai (1), Phu Hin Rong Kla (2), Na Heaw (3), Doi Luang (4), Chiang Dao Research Center (5), Doi Inthanon (6) Wieng Ko Sai (7), Khlong Lan (8). Labeled arrows indicate vectors for significant environmental variables; length of vector is proportional to the R-value

**Table 4** Non-metric multidimensional scaling correlations of abiotic factors with community composition

	$R^2$	Pr ( $>r$ )
ALL morphospecies		
Elevation	0.629	0.004***
Latitude	0.307	0.127
Longitude	0.270	0.315
Trap type	0.454	0.030**
ALL genera		
Elevation	0.087	0.359
Latitude	0.433	0.008**
Longitude	0.401	0.066*
Trap type	0.708	0.003***
LT morphospecies		
Elevation	0.544	0.013**
Latitude	0.148	0.049**
Longitude	0.304	0.282
LT genera		
Elevation	0.212	0.433
Latitude	0.241	0.401
Longitude	0.177	0.627

Correlations are listed for combined sampling (ALL) and light trap (LT) sampling

Significance of correlations was evaluated at \* =  $0.10 < P$ ; \*\* =  $0.05 < P$ ; \*\*\* =  $0.005 < P$



**Fig. 4** Non-Metric multidimensional scaling (NMDS) projection of sampling sites in northern Thailand based on morphospecies community composition. Collection codes refer to sites from: Phu Hin Rong Kla (2), Na Heaw (3), Doi Luang (4), Chiang Dao Research Center (5), Doi Inthanon (6) Wieng Ko Sai (7), Khlong Lan (8). Labeled arrows indicate vectors for significant environmental variables; length of vector is proportional to the  $R$ -value

## Discussion

This survey of North and Central Thailand discovered a crane fly fauna with higher taxonomic richness than temperate surveys covering either similarly sized sampling areas (Young and Gelhaus 2000) or comprising more intensive sampling protocols (Petersen et al. 2005). Uncovering a pattern of increased biotic diversity within the lower latitudes is not unexpected and has been reported for many taxonomic groups (Rosenweig 1995; Brown and Lomolino 1998; Willig et al. 2003). This was the first structured systematic inventory of a tropical crane fly community to consider not only taxonomic richness but also the causative agents acting to produce this diversity. By comparing the faunal assemblages of similar habitats among disjunct forest fragments, we found that the assemblages of species in northern Thailand were affected by landscape and elevation.

The high crane fly richness observed here did show community structure correlated with environmental gradients, however differences in sampling methodology may have at least partially contributed to the distinction between geographic regions. Most notable was the correlation of collection type with the separation of Khao Yai NP (1.1, 1.2, 1.3) from the remaining sites. If sampling protocol was solely responsible for the differences in community assemblage observed here, we would expect all MT collections to group together. Instead, the two collections made from Phu Hin Rong Kla NP (2.1: MT, 2.2: LT) showed higher similarity to each other and to other sites from the north, not grouping according to trap type. So, while methodology may influence the composition of fauna collected, other factors are apparently acting to shape the available fauna across the spectrum of sites sampled. Further work to examine the impact of collection methodology is needed, though our results suggest that utilizing both methods in future inventories is warranted.

Local community assemblages will be comprised of elements of surrounding regional species pools, which are in turn affected by large-scale biogeographic processes (Ricklefs and Schluter 1993; Morin 1999; Webb et al. 2002; Wiens and Donoghue 2002). The incorporation of surrounding taxon pools into the Thailand fauna may correspond to the position of the country at the intersection between different ecozones, as the fauna is comprised of groups that find their centers of diversity in either the tropics or temperate regions. The complex geological history of Southeast Asia (Hall 1998) has undoubtedly influenced the fauna of Thailand. In particular, the intersection of two corridors may help to explain the correlation of latitude to faunal composition. The mountainous north of Thailand is an extension of a continuous mountain range extending from Nepal through southwest China, northeastern India,

and Myanmar into northern Thailand. This range acts as a faunal corridor incorporating Holarctic elements into a region of tropical rain forest that extends from the south to farther north (26°N) than any place on earth (Whitmore 1990). The results of our sampling indicate that the confluence of the more tropical southern fauna and temperate northern faunas has influenced the overall crane fly community of the region, and resulted in the elevated richness seen for the country as a whole.

The altitudinal gradient of northern Thailand, acting in a similar fashion to the longitudinal gradient of the country, filters the availability of species into the local species assemblages by altering climatic and habitat types with increasing altitude. The resulting faunas are more similar at comparable elevations between mountain ranges than by geographic proximity. An influence of elevation on insect richness and community assemblage has been illustrated for many insect groups (McCoy 1990; Hodkinson 2005; Petersen et al. 2005), and this change in community assemblage may help to explain the trend of increased taxonomic richness in northern Thailand for many different groups (*owls*, *hawkmoths*, *tiger beetles*, Kitching 1996; *Lepidoptera*, Beck et al. 2007). When compared to other areas of Southeast Asia, hawkmoths (*Lepidoptera*; *Sphingidae*) and other *Lepidopteran* families reach their greatest diversity in northern Thailand due to habitat heterogeneity and the mixing of temperate and tropical faunas (Beck et al. 2007). Because of inadequate sampling across much of Southeast Asia, similar landscape comparisons beyond Thailand can not be made for crane flies. The high richness and change in community assemblages across the elevation gradient, however, does indicate that a similar Southeast Asian taxonomic hotspot may be found here.

It may be unexpected that a regional inventory will recover the entire pool of potentially available species within the study area (Preston 1948; Colwell and Coddington 1994). Therefore, the ability to provide estimates of collection rates and identify sampling success or bias will benefit future endeavors (Lewis and Basset 2007). The richness estimates offered here are still low-end approximations for Thailand, as several ecological and methodological constraints may limit our ability to evaluate crane fly richness for the entire country. Our sampling was limited to areas adjacent to aquatic systems and was focused on central and northern Thailand. The estimates of richness found here should apply only to these portions of Thailand, meaning the exclusion of expanses of southern peninsular Thailand and eastern Thailand and to species in non-aquatic ecosystems. The known immature life stages of *Limoniinae* crane flies are predominantly aquatic or semi-aquatic, but contain species that occupy purely terrestrial habitats. The terrestrial genus *Limonia*, which was previously known from Thailand, was not recollected in this

study and provides evidence that the terrestrial fauna was not sampled in this project. Expanded sampling in additional geographic and ecological areas should lead to discoveries of greater taxonomic richness in Thailand.

A major limitation to the cataloging of many faunal groups is the disparity between the location of taxonomic expertise and the epicenters of taxonomic richness. Such taxonomic hotspots are often areas of conservation importance where the ability to identify the flora and fauna are most limited due to the absence of adequate taxonomic tools. This dichotomy affects our ability to adequately infer ecological niches, community assemblage, and faunistic distribution. The investigation of sampling methodology and factors influencing community assemblages as well as the production of easily disseminated taxonomic resources, such as the taxonomic key created for this study, will serve to bridge this taxonomic divide. This increased data flow will provide a framework for future taxonomic endeavors in the region, help identify areas of increased taxonomic richness, endemism, and the causative effects that determine community structure, which will ultimately enhance further conservation efforts.

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